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THE MUTATION THEORY AND THE SPECIES- CONCEPT¹

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IN the early days of natural history, when the conceptions of special creation held sway, it was supposed that any one could determine species who was capable of observing the differences between existing forms. Linnæus crystallized this sentiment into the dictum that there are as many species as were created in the beginning, implying that any one with sufficient powers of discrimination could determine exactly how many species there were in each group. But with the introduction of the theory of evolution, species came to be viewed more and more as dynamic entities, and questions of origin have entered progressively into the species-concept. The latter has grown continually more complex, and yet Darwin's anticipation that systematists would cease to discuss how many Rubi there were in Britain or how many *Crataegi* in North America, has not been realized.

On the contrary, with this increase in the complexity of the conception of species, the extreme views as to what constitutes a species have become more and more divergent, until the "lumpers" and "splitters" among systematists usually differ radically in their interpretation of the species in a given genus. This diversity of opinion among systematists has been partly a direct result of our increasing knowledge of the complexity of species, de-

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rived from studies of variation and geographical distribution and from the experimental study of evolution.

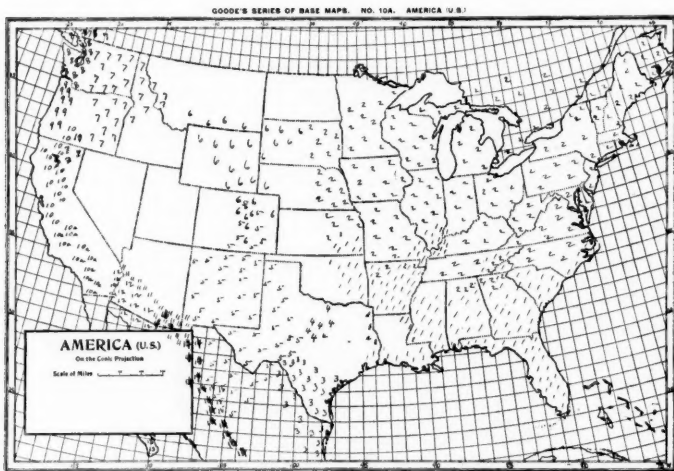


FIG. 1

Key to Map

1. *Otus asio asio* (Linn.) Ridgway (= *floridanus*).
2. *Otus asio naevius* (Gmel.) Ridgway.
3. *mccallii* (Cassin) Ridgway.
4. *hasbroucki* Ridgway.
5. *aikeni* (Brewster) Ridgway.
6. *maxwelliae* (Ridg.) Ridg.
7. *macfarlandi* (Brewster) Ridgway.
8. *kennicottii* (Elliot) Ridgway.
9. *brewsteri* Ridgway.
10. *bendirei* (Brewster) Ridgway.
- 10a. *quercinus* Grinnell.
11. *cineraceus* (Ridg.) Ridg.
12. *gilmani* Swarth.
13. *xantusi* (Brewster) Ridg.
14. *Otus trichopsis* (Wagler) Ridg.
15. *Otus vinaceus* (Brewster) Ridg.

If we look for a moment first at the complexities which have been added to the original simple concept of species, we find all grades and kinds of difference within the species itself, such as subspecies, varieties, forms and races, ending finally in the differences between single individuals. Some of these conceptions as ordinarily used are also related to geographical distribution. To them

must be added from experimental work the conceptions of mutants, Mendelian units, phenotypes and genotypes, and pure lines differing only in the position of their modal condition and requiring statistical analysis for their demonstration.

With such an array of apparently (though not really) conflicting concepts before him, it is small wonder that the systematist is inclined to cast them all aside and describe his species according to his own ideas of what they are and how they have originated. Nevertheless, for him as for the experimentalist the question What is a species? is more or less colored, if not determined by the question What is its origin? How did it appear? It might be said that the systematist should pay no attention to origins at all, merely describing what he sees. Some systematists doubtless adopt this plan. But obviously, for an understanding of the characters and relationships of species all possible facts and conceptions bearing on their origin should be considered, and in this way systematics may ultimately hope to become something more than a purely descriptive science.

If we examine the ideas which form the background of thought of the systematist in his work of constructing species, we find almost invariably that they are based entirely upon the Darwinian conception of natural selection by the gradual accumulation of slight individual differences. We are then concerned to ask, Is the systematist justified in assuming that all specific and varietal differences have originated in one way? I can find no reason in logic or philosophy why this should be the case; and for ourselves, we believe there is no single method of species formation, but we think the conclusion will ultimately be reached that the methods of species formation are multiform, though certain of them are doubtless more widespread and important than others. Among the more important factors in speciation which we wish to consider here should therefore be mentioned (1) local adaptation of races through natural selection or by direct response

to environment, (2) mutations occurring more or less independently of the environment and not necessarily of adaptive value, (3) orthogenesis, whatever that may imply. These are by no means mutually exclusive, and we can see no reason why all, and others as well which we have not time to consider, should not have been at work producing the result we call organic evolution.

It is not difficult to find, particularly among birds and mammals, instances of specific variation giving rise to local geographic races which are apparently the result of response on the part of the organism to local conditions. Again, it is easy, particularly among plants, to find varieties, species and even genera which have arisen apparently through sudden mutations and without anything in the nature of adaptational response. Finally, paleontology teems with apparent cases of orthogenetic phylogeny which are not at present clearly explainable in terms of natural selection or mutations. Before examining concrete cases which come under each of these categories let us diverge for a moment to consider the effect which natural selection as a theory has had upon biological conceptions.

We see at once that the philosophical conception of continuity took an extraordinary hold on the minds of biologists. Largely as a result of the great influence of Darwin, towards the end of the nineteenth century continuity in the origin of species became almost a fetish, and all efforts were directed to showing how every character whatsoever might have originated through the selection of a series of gradually intergrading infinitesimal steps. Yet it is more than doubtful if Darwin himself would ever have been led into such an extreme position. Biological philosophy has thus been ridden with the conception that if a character could be shown to have arisen in a gradual, piecemeal fashion its origin was thereby explained or accounted for, even though natural selection could not be shown to have operated in its development. On the other hand, the appearance of a character sud-

denly, at one step, was considered practically equivalent to its creation by a miracle, and the type of argument involving this view is still not infrequently leveled against the mutation theory.

But where lies the necessity for assuming that either continuity or discontinuity is universal? Surely the matter is one to be determined by direct observation, and not by *a priori* argument. The continuity concept of origins appears not to have influenced other sciences to the extent it has biology. True, Lyell first introduced it by developing the doctrine of uniformitarianism in geology. Nevertheless the geologist has continued to deal with large and relatively catastrophic effects occurring at irregular intervals, such as landslides, floods, earthquakes and volcanic eruptions. The phenomena of geological history are then continuous only in a limited sense.

Similarly, no chemist supposes it necessary to think that, for example, carbon and silicon were gradually differentiated from some previous substance which possessed certain qualities of both. On the contrary he sees his atoms built of definite units, the electrons, combined in various ways and numbers to give a variety of products, the elements, which are for the most part stable from the first. Hence, while perhaps little can be gained for the biologist by reasoning from analogy with other sciences, yet we at least realize that concepts of discontinuity are quite as widespread in science at large as are those of continuity, and that the origin of a character is not explained merely by breaking it up into infinitesimal steps through which it may not have passed at all.

Let us consider now some concrete instances. And here we shall select chiefly cases of discontinuity, since we are considering especially the bearing of the mutation theory on the conception of species. In examining species and genera of plants and animals, we find very often, particularly in plants, characters which almost certainly had a discontinuous origin. Perhaps the majority of generic

characters in higher plants have originated in this way. Such morphological generic characters are found in numbers wherever one turns. They indicate a great variety of marked changes, in addition to those involving alteration in number of parts; they most often concern the flower structure, on which generic differences usually depend; and in many cases at least they can not reasonably be supposed to be of any special value to the plant.

If we turn to the lily family and compare the well-known North American genera, *Smilacina* and *Maianthemum*, we find the following differences:

<i>Smilacina</i>	<i>Maianthemum</i>
Perianth segments 6	Perianth segments 4
Stamens 6	Stamens 4
Ovary 3-celled	Ovary 2-celled
Style short and thick	Style about as long as the ovary
Stigma 3-grooved or 3-lobed	Stigma 2-lobed or 2-cleft
Leaves oblong or lanceolate	Leaves usually cordate at base

These generic differences are almost entirely in the number of parts in the flower. Otherwise, in foliage and habit *Maianthemum* might be considered a reduced boreal subgenus of *Smilacina*. Can it be doubted that *Maianthemum* originated from the ancestors of certain species of *Smilacina* through a mutation, in which the flowers changed suddenly from the hexamerous to the tetramerous condition? All these changes in flower-parts would then have occurred at one stroke. It can not well be imagined that they passed through a series of gradual transition stages which have since been lost. When one remembers the almost universal occurrence of 3-parted flowers in Monocotyledons, this change becomes all the more striking. The whole order Cruciferae, among Dicotyledons, must have originated in the same way, through a sudden change from pentamery to tetamery.

If we examine the species of *Maianthemum* and their varieties we find evidence that similar processes of discontinuous variation are going on at the present time. The genus contains three species, *M. canadense* in Amer-

ica, *M. bifolium* in Europe and *M. dilatatum* in western America and northwestern Asia. *M. canadense* differs from *M. bifolium* chiefly in leaf-shape and in being typically glabrous. The pubescence probably was lost at one stroke, just as numerous glabrous varieties arise. Another step is sufficient to account for the alteration in leaf-form, so that two steps are ample for the transition from one species to the other. *M. dilatatum* resembles *M. bifolium* except for its relatively gigantic size and the fact that it is glabrous like *M. canadense*. Again two definite steps are sufficient to account for its origin.

Turning now to the geographic variations of *M. canadense* particularly as regards pubescence, a detailed study shows that over the greater part of its extensive range it is absolutely glabrous, but that pubescence has appeared especially in two localized parts of its range. A heavily hirsute variety *interius* Fernald, occurs in the Black Hills of South Dakota, an exceedingly arid region on or near the western extremity of the range of the species. This variety is apparently restricted in its distribution to the arid portion of western South Dakota, and the most reasonable interpretation appears to be that it has originated here through a marked variation, and has thus enabled the species to extend its range into this arid region. Further east, chiefly in Minnesota and Wisconsin, a semi-pubescent form occurs, and this may be the form from which the much more marked hirsute variety arose. The evidence, when closely examined, favors then a discontinuous rather than a continuous manner of origin of this heavily pubescent condition. The condition itself is nevertheless an adaptation, enabling the plant to survive in extreme conditions of aridity.

The monotypic genus *Kruhsea* is related to *Streptopus* in much the same way that *Maianthemum* is related to *Smilacina*. It was originally described in the "Flora Rossica" by Ledebour as *Smilacina streptopoides* from eastern Siberia. His name indicates his idea of its relationships. Baker afterwards, from plants without flowers

collected in Oregon, described what has proved to be the same form under the provisional name *Streptopus brevipes*. *Kruhsea streptopoides* then, although it agrees with *Streptopus* in foliage and in fruit and seed characters, differs remarkably in its flowers. They are very small, the perianth nearly rotate, dark purple; the stamens altered; and in the absence of a style the discoid stigma rests directly on the ovary. It is possible that connecting forms between *Kruhsea* and *Streptopus* may yet be found in Siberia, but at any rate the differences between these two genera can not be reasonably supposed to have arisen through natural selection. *Kruhsea* appears to have originated through a few definite germinal changes and to have since been perpetuated by heredity.

Another pair of genera which is of much interest in this connection is *Platystemon* and *Platystigma*, two Californian genera of the Papaveraceæ. Both occur abundantly as spring flowers, occupying similar habitats. Their main differences are as follows:

<i>Platystemon</i>	<i>Platystigma</i>
Stamens numerous	Stamens 6-12
Filaments broad and flattened	Filaments narrower, flattened or filiform
Carpels 6-20, forming a compound ovary, which in fruit breaks up by constrictions into 1-seeded joints	Carpels 3, forming a 1-celled, 3-valved or terete ovary which in fruit forms a 3-valved dehiscent capsule

These genera are almost exactly alike in habit, foliage, pubescence, color of flowers and general form of the stamens. They differ chiefly in the pistils, and these differences only become conspicuous as the seed capsules mature. *Platystemon* has acquired numerous carpels which are connivent or coherent in a circle. In developing, the carpels separate and their free margins cohere with each other. Each carpel then becomes torulose by constrictions between the seeds. How shall we account for the origin of such a condition except through a marked

variation, which is perpetuated by heredity and not because the plant has any advantage or disadvantage in life compared with *Platystigma*. Only one species of *Platystemon* (*P. californicus* Benth.) and two of *Platystigma* have been generally recognized, although Greene² has described some 50 species based on minor differences.

Another significant difference between *Platystemon* and *Platystigma* is in the variations of the petals. In *Platystemon* the number varies from 6 to 10 or more, and all the petals of a flower or a plant vary together in color from dark yellow through light yellow to white. In *Platystigma*, on the other hand, the number of petals appears to be uniformly six, and the outer three vary in color independently of the (alternate) inner three. Thus in *Platystigma lineare* Benth. (which Greene calls *Hesperomecon pulchellum*) the outer petals may be dark yellow, or with a more or less extensive wedge-shaped dark yellow mark at the tip, while the inner petals are light yellow or white.³

The peculiarity in the carpels of *Platystemon* acquires added interest from the fact that, as Lindley pointed out,⁴ it is by no means unique, but contraction of the sides of the carpels, forming a torulose structure, has occurred equally and must have originated independently in *Hypecoum* of the Papaveraceæ, in such genera as the radishes among Cruciferae, in *Ornithopus* among the Leguminosæ, and in other families. We may look upon this condition as apparently the result of parallel mutation in different families, independent of utility; and countless other cases of a similar kind occur among higher plants.

From the few instances I have cited, which could be added to indefinitely, and from the abundant evidence of marked variations which we have from experiment, the

² Greene, E. L., 1903, "Platystemon and its Allies," *Pittonia*, 5: 139-194.

³ A figure of *P. lineare* in *Bot. Reg.*, T. 1954 (1837), from the Russian River, Cal., shows the petals alternately yellow and white.

Another interesting point, to which Mrs. K. Brandegee has directed my attention, is the abundant occurrence of tiny plants bearing a single minute flower, intermingled with the larger plants.

⁴ *Bot. Reg.*, T. 1679 (1834).

conclusion seems clear that many marked morphological characters in plants have arisen independently of function and without the aid of natural selection. This conclusion is all the more probable because form is so much more loosely tied to function in plants than in animals. In many plants it makes little or no difference what is the shape of the leaf so far as its chlorophyllian function is concerned, nor what is the shape of the anthers so long as they produce pollen.

Another matter, which I have touched upon elsewhere,⁵ is the geographic relationships of the most closely related species of plants. It appears that Jordan's well-known law that the most nearly related species occupy adjacent areas, although widely applicable especially to the subspecies of mammals and birds, is by no means so generally true in regard to plants. But we shall come to this point again.

Referring now to animals, the North American screech owls afford an interesting case in which two kinds of variability can be clearly contrasted as regards their geographic relationships. These two types of variations are (1) those in which apparently continuous or nearly continuous variations occur progressively over certain geographical areas, with no two forms occupying the same area, and (2) those in which two or more sharply marked forms occupy the same area.

The accompanying map, compiled largely from Ridgway's data,⁶ shows the distribution of the various sub-

⁵ Gates, R. R., 1916, "On Pairs of Species," *Bot. Gazette*, 61: 177-212. Figs. 12.

⁶ Ridgway, Robert, 1914, "The Birds of North and Middle America," *Bull. U. S. Nat. Mus.*, No. 50, Part VI, pp. 882, pls. 36.

Ridgway says (p. 683): "In the main, geographic variations [in *Otus*] are more or less marked and constant; but occasionally specimens occur in a given area which are with difficulty, if at all, distinguishable from the form inhabiting another—sometimes distant—geographic area." He further comments on the fact that, while *O. choliba* in South America is remarkably uniform over a vast area, *O. asio* shows great change of coloration within relatively short distances, indicating an organization sensitive to slight changes in the physical environment.

species of *Otus Asio* Stephens (formerly known as *Megascops asio* Kaup) over the North American continent. While such a map is only approximately accurate, it shows that in general only one subspecies occupies a given geographic area.⁷ There are, however, certain exceptions. Thus in Central Colorado *Otus asio aikeni* and *Otus asio maxwelliae* both occur, the former finding here its northern limit from Texas and Mexico, the latter⁸ the southern limit of its range from Montana. It is stated, however,⁸ that they occur in Colorado chiefly at different altitudes, *maxwelliae* up to 6,000 ft. and *aikeni* from 5,000 to 9,000 ft. This is the reverse of what might be expected, since *aikeni* is the more southern form. But Mr. Aiken states⁹ that at Colorado Springs *maxwelliae* occurs only in winter and *aikeni* only in summer, indicating a slight migration. Again, *gilmani* and *cineraceus*—the latter somewhat darker with coarser pencilings and averaging slightly larger in size—both occur in southwestern Arizona, but, according to Swarth,¹⁰ although both birds may occasionally be taken in the same locality, this is only in winter when *cineraceus* comes down from the higher altitudes to the different life zone of the hot Lower Sonoran valleys occupied by *gilmani*.

The differences between these various subspecies are chiefly in density of coloration and in size.¹¹ Thus *Otus asio navius* is larger than *Otus asio asio* and is also lighter in coloration, with more white on the under parts. The subspecies *mccallii* in Texas and northern Mexico is intermediate between these in size, but is paler than either

⁷ It may be pointed out that there is sometimes discernible a tendency for systematists to call a form a subspecies or a species according to whether or not it is the only form in a given area, thus making the geographical relations of the form their criterion, rather than the degree of its distinctness.

⁸ Cooke, W. W., 1897, "The Birds of Colorado," Bull. No. 37, Agric. Expt. Sta., Fort Collins, Colo., p. 78.

⁹ Cooke, W. W., 1898, "Further Notes on the Birds of Colorado," Bull. No. 44, Agric. Expt. Station, Fort Collins, Colo., p. 160.

¹⁰ Swarth, H. S., 1916, "The Sahuaro Screech Owl as a Recognizable Race," *Condor*, 18: 163-165.

¹¹ I am indebted to Dr. Grinnell for permission to examine series of specimens in the Museum of Vertebrate Zoology of the University of California.

and more coarsely mottled. *Hasbroucki*, very limited in known range (see map), is decidedly larger and darker than *mccallii*, with much less buffy gray above and broader transverse bars. *Maxwellia*, another northern form, is decidedly larger but paler than *aikeni*. It is the palest of all in color, with more extensive pure white than even *navius*. West of *maxwellia*, in Washington and Oregon, is *macfarlanei*, which is larger and very much darker, almost agreeing in coloration with *bendirei* of California.

The Pacific coast forms comprise an interesting series running down the coast, beginning with *kennicottii*, which occurs from Sitka through British Columbia to the southern border of Washington State. It is very large like *macfarlanei*, but much darker, and browner rather than gray. The remaining subspecies extending down the coast region and into the desert become progressively paler and smaller. Thus *brewsteri* in Oregon is smaller and less brownish than *kennicottii*. In California occurs *bendirei* which is lighter again and smaller. Grinnell¹² has segregated from *bendirei* in the more arid region of southern California another form under the subspecific name *quercinus*, considered to be paler dorsally and with less or no ferruginous markings around the head. But I confess that this difference, if it exists as a constant distinction, is too fine for me to appreciate. On the contrary, specimens of *bendirei* from Palo Alto appeared to me somewhat lighter on the breast than a series from Pasadena. Whether or not this very close form is distinguishable from *bendirei*, the next in the series are *cineraceus*, *gilmani* and *xantusi*, becoming progressively lighter with finer vermiculations, the two former in southern Arizona and *xantusi* confined to the tip of the peninsula of Lower California, smaller and with the toes less feathered.

Thus the subspecies appear to be arranged progressively in passing from one geographic area to another, and there is little overlapping. But this conception of

¹² Grinnell, J., 1915, "A New Subspecies of Screech Owl from California," *Auk*, 32: 59-60.

gradual and progressive change can be overdone when it is attempted to correlate the alterations observed with climatic or other environmental features. Thus the progressive lightening in color from *kennicottii* to *xantusi*, first by lightening and restriction of the brown until it practically all disappears and then by paling and diminution of the gray, is believed to be associated with the decreasing moisture in the northern part of the range and the increasing aridity in the south. There are of course many well-known cases of paler races of birds and mammals occupying desert areas. Yet it is not clear that the coastal region of Oregon, where the less dense brown *brewsteri* occurs, is any less humid than the corresponding part of Washington where *kennicotti* is found. Similarly *xantusi* on the peninsula of Lower California can not be supposed to exist in a drier habitat than *gilmani* or *cineraceus*. Of course in none of these cases is it known just what feature in the environment acts as the critical factor nor how the race responds to it. The experimental studies of Tower¹³ and others show that a race may respond in the same way (*i. e.*, by showing the same variations) to different environmental stimuli or in different ways to the same stimulus. But studies of this character are still too few to furnish a basis for interpreting these reactions on the part of species of the higher animals. The experiments being carried on by Sumner¹⁴ with the white-footed mouse, *Peromyscus maniculatus* may be expected to throw further light on this important question of the origin of local subspecies.

Again, it is not certain that such races as *kennicottii*, *brewsteri* and *bendirei* form an absolutely graded series with all intermediates. On the contrary there appears to be some evidence that although their boundaries are contiguous there are definite though small steps from one to

¹³ Tower, W. L., 1906, "An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*," Carnegie Inst. Publ. 48, pp. 320, figs. 31, pls. 30.

¹⁴ Sumner, F. B., 1915, "Genetic Studies of Several Geographic Races of California Deer-mice," AM. NAT., 49: 688-701, with map.

the other. This may conceivably be explained through the principle of invasion and reinvasion. Grinnell,¹⁵ who is doing so much towards a detailed knowledge of the Pacific coast fauna, has considered this principle and also the part played by barriers in the development of geographic subspecies or races, in connection with the discussion of many specific cases of distribution in birds and mammals. Walter P. Taylor,¹⁶ in a recent study of the western beavers, concludes in agreement with others, that migration, geographic isolation with adaptation to local ecological niches, and final reinvasion of earlier-occupied localities, will account for the origin and present distribution of geographic subspecies such as we have been considering. This explanation seems as likely as any other at the present time, but it is beyond the purpose of the present paper to discuss these aspects of speciation in birds and mammals. The intention is rather to show that the problems involved are entirely different from those concerned with another type of variability to be mentioned in a moment. It may be pointed out, however, that although the theory of reinvasion as developed involves the conception of races isolated in certain geographic areas becoming gradually modified through environmental stress and fixed before the reinvasion takes place; that there is at the present time no definite evidence that fixation actually takes place gradually, in this way or in any other way. If intermediates between the various geographic subspecies do not occur, this may be because definite though small steps in variation are taken from one race to the other, which would do away with the necessity for assuming a long period of isolation during which the gradual development and fixation of the race

¹⁵ Grinnell, Joseph, 1914, "An Account of the Mammals and Birds of the Lower Colorado Valley, with Especial Reference to the Distributional Problems Presented." *Univ. Calif. Publ. Zool.*, 12: 51-294, 9 figs., pls. 3-13, and other papers.

¹⁶ Taylor, Walter P., 1916, "The Status of the Beavers of Western North America, with a Consideration of the Factors in Their Speciation," *Univ. Calif. Publ. Zool.*, 12: 413-495.

occurred. However, the process does appear to be gradual at least in comparison with the other type of variability, which is fundamentally different in its geographic relations.

The second type of variability in *Otus asio* to which I have reference, consists in the occurrence of gray and reddish or rufous phases of coloration in the same area of distribution. Thus all the eastern subspecies, *asio*, *navius*, *mccallii* and *hasbroucki*, produce both gray and red birds. These phases are sharply marked, and intermediates rarely occur. Hasbrouck¹⁷ attempted an explanation of this dichromatic condition, but some of his conclusions were justly criticized by Allen.¹⁸ The gray phase occurs more commonly in Florida and in the northern part of the range of *navius*,¹⁹ while the red phase occurs commonly in the Central Atlantic states, perhaps to the exclusion of the gray in some localities. The red phase is unknown in the western forms of *Otus asio*. Nevertheless grayish and rufescent phases of the small *O. flammeolus*, which is found in the mountains of western America from British Columbia to Mexico, occur in this region. The red phase is found also in *O. trichopsis* (see map). Similarly, brown and rufous phases are found in *O. choliba* which extends over a large part of South America, and also in the Central and South American species *O. cassini*, *O. guatemalæ*, *O. barbarus* and *O. vermiculatus*.

Owls belonging to other genera also exhibit two phases. For example *Bubo virginianus* (*Asio magellanicus*),²⁰ the single species of *Bubo* occurring in all North and South America, with many geographic varieties, shows dichromatism in various parts of its range. The same is apparently true of various Old World owls.

¹⁷ Hasbrouck, E. M., 1893, "Evolution and Dichromatism in the Genus *Megascops*," AMER. NAT., 27: 521-533, 638-649, 4 maps.

¹⁸ A (llen), J. A., 1893, *Auk*, 10: 347-351.

¹⁹ Oberholser, H. C., 1904, "A Revision of the American Great Horned Owls," *Proc. U. S. Nat. Mus.*, 27: 177-192.

²⁰ The red phase is stated by Allen to be rare in Maine.

Dichromatism is then, both geographically and systematically, a widespread phenomenon in owls. The red phase appears to be quite independent of geographic locality in its origin. Hasbrouck attempted to show with regard to *Otus asio* that the red phase had arisen gradually from the gray, which it was slowly supplanting in certain areas. He believed that the grays inhabited regions of greater humidity (Florida, northern range of *navius*) and the reds the drier interior, yet grays occur in Florida and reds are found, though uncommonly, in Maine. He also reported reds as occurring exclusively in the relatively humid Mississippi valley. But, as Allen pointed out, any such correlation with climatic or environmental factors hopelessly breaks down because both types are found indiscriminately over at least the greater part of the eastern range. All writers agree that the two types of plumage are independent of age, sex or season, and that in many localities at least both occur together and freely interbreed. Hasbrouck states, however, that gray males far outnumber red males, while red females outnumber gray females 4:1. Confirmation of this point is to be desired, as it suggests sex-linkage of the red condition. It is further stated that on the continent of Europe the red owls are said always to be females and the grays males.

All young birds of *Otus asio* are gray in the down, the red first appearing in the feathers. Observations go to show that red birds mated with red may give (1) all red offspring, (2) all gray, or (3) both red and gray. When one parent is red and the other gray, the same three results may follow. Further, Hasbrouck claims that gray \times gray gives always only gray young. This is probably true, but since the result is based on observation of only six matings of this kind in regions where reds occur, it is much to be desired that further observations on this point should be recorded.

The obvious hypothesis to explain these facts is that the red phase appeared as a mutation from the gray, and

that it is inherited as a simple Mendelian dominant character. The results of the various matings between red and gray would then be as stated above, according to whether the red parent were homozygous or heterozygous, but the offspring from red \times red should seldom be all gray, since this would be only a chance result when both parents were heterozygous. It is not impossible, however, since the screech owls usually have only three or four young in a nest, or sometimes only two.

Since the red phase occurs in various species as well as subspecies it is not improbable that it has originated through independent variations in different species. In any case the geographic ranges of the red phases show that, having appeared as variations, they are inherited without any conspicuous advantage or disadvantage in competition with the gray. The present frequency of the reds in certain areas and their infrequency in others may be merely an indication of the localities where the original mutations took place, and from which as centers they have gradually spread.

Although the western forms have no red phase, yet *Otus asio kennicottii* exhibits in addition to its usual tawny-brown phase a relatively rare gray phase. This fact is indeed an argument favoring the assumption that the brown phase of *Kennicottii* also arose at one step and has since nearly supplanted the original gray form.

If now we compare the two types of variability that I have described in *Otus asio*, we find them sharply contrasted in several respects: (1) the former is clearly related to geographical distribution, a single race occurring in each locality: the latter has no such relation, but two forms may occur interchangeably in the same place; (2) the former is essentially continuous as a form of variation, the latter markedly discontinuous; (3) the former appears to be related to environmental (climatic) conditions, the latter apparently bears no such relation. As regards their evolutionary significance, there can be little doubt that the former or apparently continuous type of

variations is more important in this case, for they appear to have given rise to the geographic subspecies now recognized, and, moreover, the specific differences in the genus are merely an exaggeration or intensification of the kinds of difference shown by these subspecies. It seems evident, then, that the differentiation which has gone on in the evolution of the genus *Otus* is for the most part of the kind exemplified by the small differences now existing between geographic races or subspecies occupying different areas.

The same thing is true of many other birds and mammals, but this condition is by no means universal even in these groups of animals. On the contrary, it is not difficult to find instances in which the discontinuous type of variation, independent of environment or function, has been the main factor in speciation. I will merely mention the case of the North American flickers, *Colaptes auratus* and *C. cafer*, set forth by Bateson,²¹ since the latter is a Californian bird. These species differ remarkably in their color markings, the most conspicuous differences being (1) yellow or red quills, (2) a black or a red malar strip in the males, (3) the presence or absence of a scarlet nuchal crescent in males and females. *C. auratus* possesses the first of each pair of characters and *C. cafer* the second. *C. auratus* extends from Alaska diagonally across Canada and the United States to Texas and eastward to the Atlantic, while *C. cafer* occurs in its pure form from Oregon through Utah, California and Arizona into Mexico. Each possesses 3 or 4 geographical subspecies. Where the ranges of the species overlap over a large area a mixed population of forms occurs which is usually interpreted as a series of complex hybrids, but this will bear further study. It is clear, however, as Bateson points out, that the differences in range of the species can not be associated with any constant environmental difference in the habitats, and that the species can not have differentiated from this mixed population of inter-

²¹ Bateson, W., 1913, "Problems of Genetics," Yale Univ. Press, p. 146.

mediate forms. However these species originated, they can not be reasonably supposed to have developed through gradual adaptation, but the color differences probably play no more part in the economy of the species than is the case with the red and gray phases of the screech owls. Something in the germinal organization of *Colaptes* doubtless determines the definiteness of its color patterns, and it is probable that each element of the pattern was changed by a marked step rather than through a series of gradual stages. This view is strengthened by the fact that a third species, *C. chrysoides* in Lower California, is essentially a *cafer* with yellow instead of red quills.

Thus even in birds our second type of variation, non-adaptational and not related to local conditions, is apparently an important factor in speciation, although in *Colaptes* too geographical races occur as well. In distribution also these species do not follow the rule for geographic subspecies, for they overlap over large areas. The fact that each species has its own geographic subspecies shows that the origin of these species antedates the development of their geographic varieties.

I have endeavored to show that in plant and animal species there are two distinct types of variability, having different geographical relations. The one is discontinuous, independent of environmental or functional influence, and has given rise to many specific and generic characters, notably in plants but also in higher animals. The other is continuous and apparently represents the results of the stress of the environment on the species in its dispersal, leading to the gradual differentiation of local races or subspecies whose peculiarities are ultimately intensified and fixed. The latter type of speciation is notably exemplified in birds and mammals, organisms in which, unlike plants, the individuals can migrate from place to place and so substitute for a stress resulting from overpopulation an environmental stress caused by a new set of climatic or physiographic conditions.

FURTHER OBSERVATIONS ON THE EFFECTS OF ALCOHOL ON WHITE MICE¹

L. B. NICE

IN a former paper ('11) it was found that white mice were not markedly affected when given alcohol in their food. Since this paper appeared Stockard ('12, '13, '16) has brought forth some striking and conclusive results demonstrating that guinea pigs are very sensitive to alcohol and decidedly injured by it. He administered the alcohol to his animals through the lungs by placing them in a tank containing alcohol at the bottom so that they had to inhale the fumes. His work raised the question as to whether similar results might be obtained with white mice by using the same method. Therefore it was decided to repeat my experiments, using the inhalation method.

For these experiments white mice eleven weeks old were obtained. They were all from one strain inbred to the fourth generation, two entirely distinct strains having been united to form this strain. They were divided into four lines, viz., a control line, a double alcohol line, that is, both males and females were subjected to alcohol, a female alcohol line and a male alcohol line. There were three cages in each line, each cage contained two females and one male, thus making six females and three males in each line. Two cages were made up of second generation alcoholized mice; both males were from the male alcohol line, two females from the same line and one female from the female alcohol line. The same cages were used as in my former experiments. They were made of 8-mesh wire and were 6 inches wide, 6 inches deep and 12 inches long.

The mice were kept in a laboratory room heated by steam. It was attempted to keep the room at a uniform temperature, but fluctuations occurred.

¹ From the Laboratory of Physiology in the University of Oklahoma. For a review of the literature see Nice ('11 and '12). Also Stockard ('12, '13 and '16).

All the animals were fed the same food, consisting of wheat and kaffir corn with bread and milk once a day.

Every day except Sunday the double alcohol line, parents and young, the males of the male alcohol line, the females and young of the female alcohol line and the second generation of alcohol mice with their young were placed in a galvanized tank 26 inches long, 20 inches wide and 14 inches deep. Alcohol had been poured on to cotton which was placed under a wire mesh situated about 2 inches from the bottom of the tank, so the mice had to breathe the fumes. The mice were kept in the tank each day until they became intoxicated, as shown by their staggering gait or inability to stand up. At the beginning of the experiment the time necessary to intoxicate them was about one hour. Later they would often be kept in the tank for two hours. This shows that the mice acquired a tolerance for alcohol. This tolerance was shown after they had been treated about a month. To make sure that the mice were being heavily alcoholized, a few times they were left in the tank so long that they would not recover from the effects for three or more hours, and in some cases they did not recover from the intoxication, but died.

At the beginning of the experiment when the mice were placed in the alcohol tank they would sneeze, their eyes water and they would rush about in their cages, showing great uneasiness. Later they ceased to be so much disturbed, yet during the course of the experiment there was no indication that the mice liked the alcohol fumes.

THE WEIGHT OF THE ADULT MICE

The adult mice were weighed at the beginning of the experiment and once each month thereafter, to get an indication as to their health. Since they were nearly the same age and closely related, their average weights would be expected to be about the same unless the alcohol treatment had an injurious effect on them. By referring to Table X, it will be seen that there is only a slight difference between the various lines. The average weight

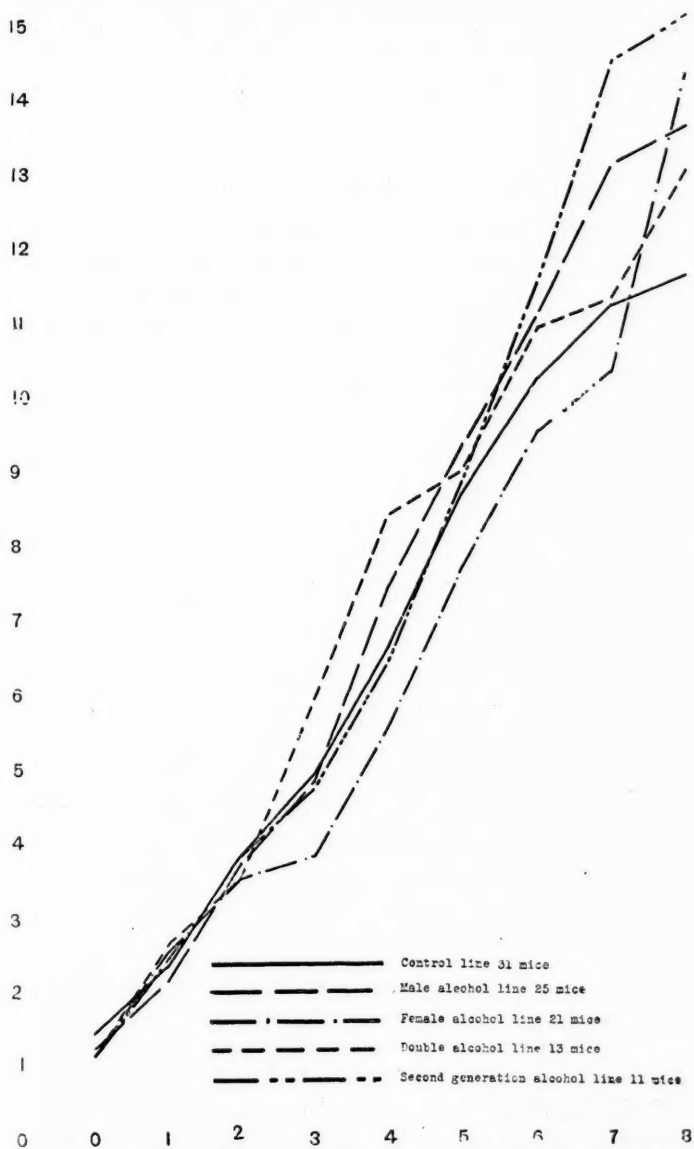


FIG. 1. Curve showing the growth of the mice. The abscissas represent the age of the mice in weeks and the ordinates their weights in grams.

of the mice not treated with alcohol was 22.4 grams and of those treated with alcohol 21.8 grams.

TABLE I
AVERAGE GAINS OF ADULT MICE
Those Not Given Alcohol

Line	Sex	No. of Mice Weighed	Average Gain in Grams at 4 Months	No. of Mice Weighed	Average Gain in Grams at 7 Months
Control.....	Male	3	4.6	3	4.9
Control.....	Female	6	4.3	6	9.3
Male alcohol.....	Female	6	4.3	6	6.4
Female alcohol.....	Male	3	5.8		
Average gain of all mice not given alcohol.....		18	4.6	15	7.2

TABLE II
AVERAGE GAINS OF ADULT MICE
Those Treated with Alcohol

Line	Sex	No. of Mice Weighed	Average Gain in Grams at 4 Months	No. of Mice Weighed	Average Gain in Grams at 7 Months
Double alcohol.....	Male	3	3.2	1	4.0
Double alcohol.....	Female	8	4.8	2	4.2
Male alcohol.....	Male	3	3.0	3	3.5
Female alcohol.....	Female	4	3.5		
Average gain of all mice given alcohol.....		18	3.9	6	3.8

Tables I and II give the average gain of the different lines for four months and for seven months. The mice that did not receive alcohol gained more than those that were treated; the former gaining 4.6 grams on an average for four months and the latter 3.9 grams; in seven months the untreated mice gained 7.2 grams and the alcoholized 3.8 grams.

It is possible that the handling of the mice and the extra exercise they took in the excitement of being alcoholized might account in part for their growing less than the untreated mice. In the 1911 experiments the control mice carried 7 months gained only 2 grams on an average while the alcohol mice gained 6 grams; in the second generation carried four months the controls gained 1 gram each and

TABLE V
FEMALE ALCOHOL LINE

Female	No. of Mo. Observed	No. of Litters	No. of Young Born	No. of Young That Died
A.....	4	1	7	0
B.....	4	1	7	0
C.....	4	2	12	3
D.....	4	2	15	1
E.....	2	0	0	0
F.....	2	0	0	0
Total.....	4:4 2:2	6	41	4

Note.—Females *A*, *B*, *C*, and *D* were killed by being left in the alcohol tank too long. Females *E* and *F* were killed by accident.

TABLE VI
DOUBLE ALCOHOL LINE

Female	No. of Mo. Observed	No. of Litters	No. of Young Born	No. of Young That Died
A.....	4	1	5	0
B.....	4	1	7	0
C.....	9	0	0	0
D.....	9	3	20	0
E.....	4	2	15	2
F.....	4	2	15	0
G.....	4	1	5	1
H.....	4	1	6	2
Total.....	6:4 2:9	11	73	5

* These mice from *A* to *F* were left in the alcohol tank so long one day that only *C* and *D* survived the experience. After this accident one more cage, *G* and *H*, were made up from the original stock.

TABLE VII
SECOND GENERATION ALCOHOL LINE

Female	No. of Mo. Observed	No. of Litters	No. of Young Born	No. of Young That Died
A.....	2½	1	6	1
B.....	2½	1	10	0
C.....	2½	1	9	0
Total 3.....	2½	3	25	1

VIABILITY OF THE YOUNG

Table VIII shows the number of litters and the number of young born in each line; also the number that died from lack of vitality.

the alcohol mice 2 grams. In that case the alcohol was given in the food and water and apparently had a fattening effect. None of those animals were handled except for weighing them.

RECORDS OF THE YOUNG OF EACH FEMALE

A record was kept of the young of each female. Many of the young in each of the lines were eaten by their parents. Tables III to VIII show the number of months each female was carried; the number of litters each had; the total number of young born, and the number that died apparently from lack of vitality.

TABLE III

RECORD OF THE YOUNG OF EACH FEMALE CONTROL LINE

Female	No. of Mo. Observed	No. of Litters	No. of Young Born	No. of Young That Died
<i>A</i>	7	1	7	0
<i>B</i>	7	2	10	0
<i>C</i>	7	1	6	0
<i>D</i>	7	1	5	0
<i>E</i>	7	1	6	0
<i>F</i>	7	1	2	0
<i>G</i> *.....	4	1	6	0
<i>H</i> *.....	3	1	5	0
Total.....	6:7 1:4 1:3	9	47	0

* Females *G* and *H* are second generation controls.

TABLE IV

MALE ALCOHOL LINE

Female	No. of Mo. Observed	No. of Litters	No. of Young Born	No. of Young That Died
<i>A</i>	7	2	12	1
<i>B</i>	7	1	12	0
<i>C</i>	7	2	10	0
<i>D</i>	7	1	3	3
<i>E</i>	7	1	5	0
<i>F</i>	7	3	24	0
Total.....	7	10	66	4

TABLE VIII
RECORD OF THE YOUNG OF EACH LINE
Summary of Tables III to VII

Line	No. of Mice	No. of Months	No. of Litters	No. of Young	No. That Died	Per Cent. That Died
Control	{ 6 1 1	7 4 3	9	47	0	0
Male alcohol.....	6	7	10	66	4	6
Female alcohol.....	4	4	6	41	4	9.8
Double alcohol.....	{ 6 2	4 9	11	73	5	6.8
Second generation alcohol.....	3	2½	3	25	1	4

As in my former experiments none of the control young died of lack of vitality. The alcohol lines show a small percentage of deaths—4 mice or six per cent. in the male alcohol line, 5 mice or 6.8 per cent. in the double alcohol line and 4 mice or 9.8 per cent. in the female alcohol line. The second generation alcohol lines had 1 death or 4 per cent. of all of their young. In the former experiments ('11) the fatalities were somewhat greater—9 young or 11.1 per cent. in the first generation of alcoholized mice and 7 young or 12.5 per cent. in the second generation. Stockard ('16), with his guinea pigs, had a fatality of 43 per cent. in the male alcohol line, 52 per cent. in the female alcohol line, 46 per cent. in the double alcohol line and 16 per cent. in the control line.

FECUNDITY

Table IX gives the average number of litters, average number of young, and average number in a litter for one female of the control line and one female of the male alcohol lines for seven months; for one female of the female alcohol line and double alcohol line for 4 months; and for the second generation alcohol line for 2½ months.

On account of the difference in the length of time the different lines were carried, it is impossible to make a direct comparison. However the greater fecundity of all the alcohol lines over the control line is striking. Though

TABLE IX
FECUNDITY OF THE DIFFERENT LINES
Average of One Female of Each Line

Line	Months Observed	Average in a Litter	Average No. of Litters	Average No. of Young
Control.....	7	5.1	1.3	6.5
Male alcohol.....	7	6.6	1.66	11.0
Female alcohol.....	4	6.83	1.5	10.25
Double alcohol.....	4	6.5	1.4	9.3
Second generation alcohol.....	2½	8.3	1.0	8.3

the control mice were carried longer than any line except the male alcohol line, they have next to the lowest number of litters—the lowest being the second generation alcohol line carried only one third as long as they. They have the fewest young of all the lines and the smallest litters. The male alcohol line can be compared directly with the control line since they were both carried seven months. They have somewhat larger litters, somewhat greater average number of litters and nearly twice as many young as the controls. It is not possible to compare them directly with the lines that were only carried four months, but since the averages of these lines are almost as high as those of the male alcohol mice, it follows that the male alcohol mice were not as fecund as the female alcohol and double alcohol lines. The female alcohol mice show the greatest fecundity of all the lines, while the double alcohol and second generation of alcohol mice come next.

The three lines in which the females were alcoholized were somewhat more fecund than the line in which the males alone were alcoholized and decidedly more so than that in which neither parent was alcoholized. These results confirm those obtained in my former work ('11) where the control mice carried 7 months had 2.2 litters or 13.3 young on an average and the alcohol mice had 2.8 litters and 16.1 young; the second generation of control mice carried 4 months had 1.5 litters and 7.1 young, while the corresponding alcohol line had 1.8 litters or 12.4 young.

Why the mice had fewer young in these experiments

than in the former is not clear. It may have been due in part to the greater fluctuations of temperature in the laboratory building used here. Whatever the reason, the control mice in these experiments after the first few months occupied themselves in growing fat instead of having young.

Stockard's results on guinea pigs are directly contrary to these; his alcoholized animals had decidedly fewer young than the control guinea pigs.

COMPARISON OF THE GROWTH OF THE YOUNG IN THE VARIOUS LINES

In comparing the weights in Table X and Curve I it should be remembered that all of these young were alcoholized except the male alcohol line and of course the controls.

TABLE X
WEEKLY GROWTH OF THE YOUNG

Line	Average Weight of Female Parents	Average Weight of Male Parents	Number of Young Weighed	Average Weight per Mouse at Birth	Average Weight at One Week	Average Weight at Two Weeks	Average Weight at Three Weeks	Average Weight at Four Weeks	Average Weight at Five Weeks	Average Weight at Six Weeks	Average Weight at Seven Weeks	Average Weight at Eight Weeks
Controls.....	22.6	21.5	31	1.4	2.3	3.8	4.9	6.6	8.7	10.2	11.2	11.6
Male alcohol.....	23.2	24.8	25	1.2	2.1	3.7	4.8	7.4	9.3	11.1	13.1	13.6
Female alcohol.....	20.2	21.4	21	1.1	2.5	3.5	3.8	5.5	7.7	9.5	10.3	14.3
Double alcohol.....	21.1	23.7	13	1.2	2.6	3.5	5.9	8.4	9.0	10.9	11.3	13
Second generation alcohol...	13.5	17	11	1.1	2.4	3.8	4.7	6.4	8.8	11.5	14.5	15.1

The weights of all the lines at birth and for the first two weeks are quite similar. After that variations began. The young of the double alcohol line surpassed all for four and a half weeks, while the young of the female alcohol line fell behind all the others at the beginning of the third week and remained below up to the seventh week and at the eighth week they were next to the highest. The young of the control line, the male alcohol line and the second generation of the alcohol line grew at about the same rate up to the fifth week. At this time the weight of the male alcohol line slightly surpassed all the others; then the

second generation of alcohol mice outgrew all and continued ahead until the end of the experiment. After the sixth week there were rather wide variations and this continued as long as they were weighed. At the eighth week the weights of the different lines stood in the following order: second generation of alcohol mice 15.1 grams; female alcohol mice 14.3 grams; male alcohol mice 13.6 grams; the double alcohol mice 13 grams; and the controls 11.6 grams. In my former experiments ('11) the alcohol young surpassed the controls in the rate of growth.

COMPARISON OF THE DIFFERENT LINES

The control line had the fewest young of any of the lines; they had no deaths from lack of vitality; the growth of their young was slower than that of any of the other lines except the female alcohol line.

The male alcohol line was more fecund than the controls, but less so than the other alcohol lines; their death rate from lack of vitality was four mice or 6 per cent.; the growth of their young was better than that of the controls and female alcohol lines.

The female alcohol mice were the most fecund of all the lines; their death rate was four mice or 9.8 per cent.; their growth was even slower than the control mice until the last week, when they made a large gain and outgrew all but the second generation of alcohol mice.

The double alcohol mice were slightly less fecund than the female alcohol line; five mice or 6.8 per cent. of their young died; they grew a little faster than the controls.

For the second generation of alcohol mice, two males, offspring of the male alcohol line, were mated with two females, young of the same line and one female from the female alcohol line. Thus one grandmother and all but one of the grandfathers were alcoholized, the second generation were all alcoholized after they became adult and one from birth and their young also were alcoholized. The fecundity of the second generation of alcohol mice was high; they had one death from lack of vitality, or 4

per cent. of all their young, and their young grew the fastest of all the lines.

It is a matter of regret that owing to an accident—over-alcoholization one day—the second and third generations were not carried farther. However, as far as they went, no injurious effect from alcohol is apparent in fertility, nor vigor of growth, and but a small one in viability.

From indications in our results it would seem to be dangerous to draw far-reaching conclusions from data obtained on a single species. Although this work was not carried as long as it was planned, yet as it corroborates my former experiments in practically every detail it goes to prove that mice are to a degree resistant to alcohol whether it is fed or inhaled by them. From results obtained in bacteriological laboratories it is well known that mice are very resistant little animals, in comparison to sensitive animals like guinea pigs. Mice are immune to the toxin of the tetanus bacillus. It seems reasonable to expect that an animal which is immune to such a virulent toxin might have a considerable degree of resistance to the effects of alcohol.

SUMMARY

1. The white mice given alcohol by the inhalation method gave much the same results as those that received it in their food in my former experiments.

2. The fecundity of the alcohol mice was greater than that of the control mice, as in my former study.

3. Six per cent. of the young of the male alcohol line, 6.8 per cent. of the double alcohol line, 9.8 per cent. of the female alcohol line and 4 per cent. of the second generation alcohol line died from lowered vitality, while none of the control young died. Similar results were obtained in my former experiments, except that the alcohol line had a higher death rate—11.1 per cent. in the first generation and 12.5 per cent. in the second generation.

4. The growth of the young of all the alcohol lines ex-

ceeded that of the controls, as in my former experiments. The young of the second generation alcohol line outgrew all the others.

5. There were no abortions, no still births and no monsters obtained in these experiments, nor in the former.

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LINKAGE IN LYCOPERSICUM

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THE known cases of linkage of hereditary factors in plants are not as yet so numerous but that it seems desirable to place on record all instances of this condition. With that end in view I wish to call attention to some scattered data obtained several years ago, before much was known about linkage, and presented in publications which are probably not widely circulated.

Part of the data to be considered resulted from an investigation, started by Hedrick and Booth, shortly after the beginning of the awakened interest in Mendelism, which was designed to test the inheritance of Mendelian characters in the garden tomato (*Lycopersicum esculentum* Mill.). The results were published in the *Proceedings* of the Society for Horticultural Science in 1907. Two different crosses were studied. One cross was made between two varieties which differed in one character only, viz., standard and dwarf habit of vine. The other cross was between two varieties which differed in three characters, habit of vine, shape of fruit and color of fruit. It is this second cross which gives evidence that there is a genetic linkage between the factors for habit of vine and shape of fruit.

In this latter cross the varieties used are known under the varietal names of Quarter Century and Yellow Pear. The Quarter Century variety is described as having a dwarf type of vine, red-colored fruit which is shaped like that of the common garden varieties, *i. e.*, more or less spherical. The Yellow Pear variety has a standard or spreading vine, fruit yellow in color and pear-shaped.

The first generation plants grown from this cross were standard in habit of vine, with red-colored fruit which differed in shape from either parent, being oval rather

From the results as given it can be seen that the plants with the combinations of habit of vine and shape of fruit obtained in F_2 which duplicated the parental combinations, are more numerous than expected, whereas the two new combinations, with respect to these two factors, are less than expected. The writers observed these facts and commented upon them as follows:

The percentage of plants which fall into each class are, however, quite different from those of Mendel. This is of importance in that it indicates the number of plants which it is necessary to grow in order to get a plant with a certain combination of characters. Theoretically, 64 plants should have included all the combinations we secured; actually, with 452 plants there is one combination with only one representative. In place of one representative, there should have been seven. Our results would indicate that it is necessary to raise seven times as many tomatoes as are theoretically necessary in order to secure a desired combination. There is apparently a method to this variation. *The tendency seems to be for the second generation hybrids to go back to the same combinations of characters as the parents, rather than to form new ones.*¹ Thus it will be seen that the tomato with Quarter Century fruit on Yellow Pear vines is less than theoretical considerations alone would indicate, while the number of tomatoes with Quarter Century fruit on Quarter Century vines is more than theory would require; the same being true for the yellow pear. Inertia seems to be a factor and the preservation of the *status quo* an object among tomatoes as among men (p. 23).

In the light of more recent investigations of factorial linkage it is recognized at once that the above statement fulfils the conditions of linkage between at least two of the allelomorphic pairs concerned. Let us then examine the data more closely to see if a clear case of linkage can be made out.

Since the deviations above and below the expectancies are about the same in both the red-fruited and yellow-fruited plants, it indicates that color of fruit is an independent factor and that habit of vine and shape of fruit are partially linked with frequent breaks in the linkage. Combining the figures for yellow and red fruit and putting the 452 plants into 6 categories instead of 12, the condensed results given in Table II are obtained.

¹ The italics are mine.

tion by the man pricking out the young plants from the seed boxes, of the larger, that is, the standard plants. This point had been anticipated and the workmen cautioned to take the plants just as they came, but it is against all of a gardener's training to throw aside a good vigorous plant and take one half the size.

However, in the F_3 plants given above, from F_2 segregating plants, all the seeds which were planted and lived were grown to maturity, so that the latter source of error, of unequal sampling, was avoided. Still there was the same deficiency of dwarfs.

Craig (1907), in the same publication, reports large numbers of the same cross which also showed a deviation in the second generation, of too many standard plants. He does not state whether or not an attempt was made to grow all the plants obtained from the seed planted. His figures are as follows:

	Found	Expected
Stone \times Dwarf Aristocrat, F_2 : Standards	2,499	2,367
Dwarfs	657	789
Stone \times Dwarf Aristocrat, F_3 : Standards	154	155
Dwarfs	52	51

Both Halsted (1905) and Price and Drinkard (1908) give figures on the proportions of standard and dwarf plants obtained in F_2 populations. I have tabulated their data as follows:

Halsted's Data (pp. 450-462)

	Standards	Dwarfs
Dwarf Champion \times Magnus, F_2	65	20
Dwarf Stone \times Golden Queen, F_2	25	5
Dwarf Stone \times Extra Early Tree, F_2	14	6
Lemon Blush \times Dwarf Champion, F_2	18	3
Total found	122	34
Expected	117	39

Price and Drinkard's Data (Table XI, p. 40)

	Standard	Dwarf
Dwarf Champion \times Red Currant	21	3
Potato Leaf \times Dwarf Champion	15	9
Total found	36	12
Expected	36	12

In these last two tabulations many of the crosses show a deficiency of dwarfs, although the results as a whole agree closely with expectations. However, the numbers are too small to place much weight upon.

In connection with another investigation I have obtained considerable data on the inheritance of this character, by simply growing the seedlings in flats from 6 to 8 weeks, and then counting the dwarfs and standards without setting the plants in the field, as in all the previous cases cited. It is not always possible to distinguish all of the two types of plants, with certainty, at this stage especially, if the plants are crowded and there are many small stunted plants. However, counting the plants at this time removes the possibility of unequal sampling when only a part of the seedlings are set in the field, and also the possibility of differential viability in the field. The distributions in 5 F_2 and 16 F_3 populations from heterozygous F_2 plants gave the following results:

	Standards	Dwarfs
Dwarf Champion \times Stone, 5 F_2 populations	1,103	437
Dwarf Champion \times Earliana, 1 F_2 population ...	186	67
Dwarf Champion \times Stone, 12 F_3 populations ...	1,707	730
Dwarf Champion \times Earliana, 4 F_3 populations ..	571	149
Total found	3,567	1,383
Expected	3,713	1,237

Here the deviation from expectation is in the opposite direction. There is an excess of dwarfs. It would seem that too many of the small plants were classified as dwarfs when they were really standards. Two of the above F_2 populations were grown longer than the others in flats which were not so crowded, so that the errors in classification, I believe, were more nearly overcome. The following results were obtained:

	Standards	Dwarfs
Dwarf Champion \times Stone, F_2	268	88
Dwarf Champion \times Earliana, F_2	186	67
Total found	454	155
Expected	457	152

From these data it seems justifiable to conclude that dwarfness and standardness form a simple allelomorphic pair, free from any genetically complicating factors.

I have gone to this length to demonstrate the normal behavior of this character in order to be able to correct Hedrick and Booth's data according to the proportion of dwarf and standard plants, which presumably they should have obtained if all the plants had been grown to maturity, and if there had been equal viability. Moreover, whether or not the deficiency of dwarfs which they obtained is due to unequal sampling, differential viability or some unknown cause, there is no reason to suppose that the cause, whatever it is, has anything to do with the linkage between the factors for habit of vine and shape of fruit. I have, therefore, in Table III increased the num-

TABLE III
CORRECTED DISTRIBUTION OF THE F_2 PLANTS WITH RESPECT TO THEIR
HABIT OF VINE AND SHAPE OF FRUIT—CHARACTERS
WHICH SHOW LINKAGE

Genetic Formu- lae	Characters of F_2 Plants	1. Found	2. Expected	3. Corrected	4. Expected	Combinations of Characters
AB....	Standard vine, non-constricted fruit	252	254	252	284	New combination
Ab.....	Standard vine, constricted fruit.....	127	85	127	95	Parental combination
aB.....	Dwarf vine, non-constricted fruit...	70	85	121	95	Parental combination
ab.....	Dwarf vine, constricted fruit.....	3	28	5	31	New combination
	Total.....	452	452	505	505	

ber of dwarfs to the number theoretically expected, keeping the proportion of the two different kinds of dwarfs the same with respect to shape of fruit. From Table II it can be noted that 379 standards were obtained. Theoretically the dwarfs should have been one third of this number, or 126.3. There were actually only 73. This number would have to be increased 1.73 times in order to bring the number of dwarfs up to the expected number. Combining both the standard and dwarf plants in two classes each, those with and those without constricted fruit, and multiplying these two classes of dwarf plants

by 1.73, the figures given in column 3 of Table III are obtained. The figures in this column represent the number of plants which presumably should have been obtained in the four different categories, if the expected number of dwarf plants had been obtained.

These corrected numbers can then be compared with the closest theoretical ratio where the gametes, instead of being produced in the equal proportion of 1 AB:1 Ab:1 aB:1 ab, were produced in unequal proportions (where A and B represent the two dominant factors—standard vine and non-constricted fruit). In this case if the gametes were formed in the proportion of 1 AB:4 Ab:4 aB:1 ab, the agreement between the corrected result and the theoretical expectation is surprisingly close.

	AB : Ab : aB : ab
Corrected numbers	252 : 127 : 121 : 5
Corrected ratio	50.4 : 25.4 : 24.2 : 1
Theoretical ratio	51 : 24 : 24 : 1
(1:4:4:1 gametic series)	

It is seen that the data obtained by Hedrick and Booth give a clear indication of linkage of the factor for standard vine with that for constricted fruit and dwarf vine with non-constricted fruit. Frequent breaks in the linkage occur to form the two new combinations. On the chromosome hypothesis the data show, in this case, that crossing over occurs in 20 per cent. of the gametes formed.

TABLE IV
CORRECTED DISTRIBUTION OF THE F_2 PLANTS WITH RESPECT TO THEIR
HABIT OF VINE AND COLOR OF FRUIT—CHARACTERS WHICH
DO NOT SHOW LINKAGE

Genetic Formulae	Characters of F_2 Plants	1. Found	2. Expected	3. Corrected	4. Expected	Combinations of Characters
AB....	Standard vine, red fruit.....	294	254	294	284	New combination
Ab....	Standard vine, yellow fruit.....	85	85	85	95	Parental combination
aB....	Dwarf vine, red fruit.....	56	85	97	95	Parental combination
ab....	Dwarf vine, yellow fruit.....	17	28	29	31	New combination
	Total.....	452	452	505	505	

The data also show that there is no linkage between the other two combinations of factors reported, viz., vine habit and fruit color, and fruit color and fruit shape. Correcting the number of dwarfs in the same way as in Table III the results for these two combinations of factors are given in Tables IV and V.

TABLE V

CORRECTED² DISTRIBUTION OF THE F₂ PLANTS WITH RESPECT TO THEIR SHAPE OF FRUIT AND COLOR OF FRUIT—CHARACTERS WHICH DO NOT SHOW LINKAGE

Genetic Formula	Characters of F ₂ Plants	1.	2.	3.	4.	Combinations of Characters
		Found	Expected	Corrected	Expected	
AB....	Non-constricted, red fruit	250	254	289	284	Parental combination
Ab.....	Non-constricted, yellow fruit.....	72	85	84	95	New combination
aB.....	Constricted, red fruit	100	85	101	95	New combination
ab.....	Constricted, yellow fruit.....	30	28	31	31	Parental combination
	Total.....	452	452	505	505	

From these two tabulations it will be seen that the agreement between expectation and observation, when the number of dwarfs is increased to the number expected, is reasonably close, and the deviation from the expected is not such as to suggest linkage between any of these factors.

Both Halsted, and Price and Drinkard, in the publications previously mentioned, give a large number of crosses of tomatoes where the inheritance of many different characters are studied. Unfortunately, in most cases the data are presented in such a way as to show the inheritance of only one character pair at a time.

Halsted gives a dihybrid cross between two varieties differing in habit of vine—standard (A) and dwarf (a), and margin of leaf—serrate (B) and entire (b). The

² Since habit of vine is not concerned in this cross it is, of course, unnecessary to correct for the low number of dwarfs as in the two previous tables. I have done so simply to show that it does not affect the goodness of fit to any great extent.

cross was made in such a way that one dominant factor entered from each parent. The numbers obtained

	AB: Ab: aB: ab
Found	49: 16: 13: 7
Expected	48: 16: 16: 5

do not indicate any linkage between these factors.

Price and Drinkard's data indicate that there is no linkage between shape of fruit and color of fruit in two different crosses (agreeing with the data given in Table V), none between foliage color and fruit color, and none between foliage color and fruit shape. In these crosses the numbers are too small to be sure of the conclusions with regard to linkage. They give the results of a cross, however, which shows complete linkage between green foliage color and two-celled fruit, as opposed to yellow foliage color and many-celled fruit. Only 24 F_2 plants were grown, which were of two types only, duplicating the parents.

These characters, foliage color and loculation of ovary, can not be the expression of the same factor because many varieties are known with these characters combined in the other ways. In fact the majority of the common garden varieties have green foliage and many-celled fruit. Neither does it seem probable that these dissimilar characters form a series of multiple allelomorphs as some cases of complete linkage, for instance, cob and pericarp colors in maize, are considered to be. Although the number of plants is small, as the writers state, it would seem that among 24 plants at least one new combination would appear if the factors were independent of each other. Larger numbers of a similar cross, studied by back crosses in the more favorable way, will probably show these factors to be partially linked.

Crane (1915) reports a cross between varieties of tomatoes differing in rather complex characters of inflorescence and fruit shape. He obtained figures which indicate partial linkage in these characters, but states that "the

numbers are not sufficiently large to form any conclusion as to the intensity of the coupling, nor to establish the existence of the same with certainty."

A number of clearly segregating characters are known in the tomato. Halsted lists 7 alternative unit character pairs, while Price and Drinkard give 13. However, from their own statements in regard to the behavior of these characters, and from my own rather limited experience with tomatoes, the number of different character pairs which they list should be reduced. For instance, only two allelomorphic pairs are known for color of fruit, viz., red and yellow flesh or endocarp, and yellow and colorless fruit skin or epicarp, while Price and Drinkard give four, and Halsted three, character pairs of fruit color. Different combinations of skin colors and flesh colors give the different colored fruits. For example, colorless epicarp over red endocarp gives pink-colored fruit.

TABLE VI

MEDELIAN CHARACTERS IN THE GARDEN TOMATO
(Revised from the lists given by Halsted and by Price and Drinkard.)

		Dominant	Recessive
Fruit shape.....	1	Spherical (non-constricted).....	Pyriform (constricted)
Fruit shape.....	2	Roundish conic.....	Roundish compressed..
Loculation of ovary.....	3	Bilocular.....	Plurilocular.....
Endocarp color.....	4	Red.....	Yellow.....
Epicarp color.....	5	Yellow.....	Colorless.....
Fruit surface.....	6	Smooth.....	Pubescent.....
Vine habit and leaf surface.....	7	{ Standard.....	{ Dwarf.....
Leaf margin.....	8	{ Smooth.....	{ Rugose.....
		Serrate (normal or fine leaf).....	Entire ("potato" or coarse leaf).....
Leaf type.....	9	<i>Pimpinellifolium</i> type..	<i>Esculentum</i> type.....
Foliage color.....	10	Green.....	Yellow.....
Inflorescence type ³	11	Simple.....	Compound.....

It is somewhat uncertain as to the number of independent factors concerned in fruit shape. According to Crane (*loc. cit.*) and Groth (1912 and 1915) there are a number of factors and it is not always possible to distinguish between the various shapes. There is apparently a corre-

³ See Crane, 1915, p. 4.

lation between the loculation of the ovary and some fruit shapes, although not necessarily with the constricted type of fruit. The foliage characters (Groth, 1911) are rather complicated. Also the color of foliage and the color of the epicarp of the fruit may be associated in the same way that habit of vine and leaf surface are, *i. e.*, the expressions of one factor. Dwarf plants always have a more rugose foliage than standard plants. According to Groth (1915, p. 17) dwarfness can not be associated with pubescent fruit for some reason.

A list of the Mendelian genes, so far known in the tomato, is given in Table VI.

The list is only tentative. A more detailed study of these characters will probably necessitate further revision. Other character differences may be known and should be added. There are, however, at least 10 plainly segregating genes and probably more. The behavior of 6 of these with respect to their being linked or not linked with each other, in all the 15 possible combinations,⁴ is known in the case of 7 of them and can be predicted for 5 others. These 15 combinations with respect to linkage are summarized as follows:

CHARACTERS SHOWN TO BE LINKED FROM THE DATA OF HEDRICK AND BOOTH,
AND PRICE AND DRINKARD

Vine Habit,	7	with	Fruit Shape,	1
Foliage Color,	10	with	Loculation of Ovary,	3

CHARACTERS SHOWN NOT TO BE LINKED FROM THE DATA OF HEDRICK AND
BOOTH, HALSTED, AND PRICE AND DRINKARD

Vine Habit,	7	with	Endocarp Color,	4
Vine Habit,	7	with	Leaf Margin,	8
Fruit Shape,	1	with	Endocarp Color,	4
Fruit Shape,	1	with	Foliage Color,	10
Endocarp Color,	4	with	Foliage Color,	10

⁴ The possible number of combinations is obtained from the formula $\frac{n^2 - n}{2}$ where n^2 equals the total number of combinations, two at a time, between n different units but no factor can, of course, be paired with itself and the remaining pairs are duplicated.

CHARACTERS WHICH CAN NOT BE LINKED (ON THE CHROMOSOME HYPOTHESIS
IF THE ABOVE CASES HOLD TRUE)

Endocarp Color,	4	with	Loculation of Ovary,	3
Vine Habit,	7	with	Loculation of Ovary,	3
Vine Habit,	7	with	Foliage Color,	10
Fruit Shape,	1	with	Leaf Margin,	8
Fruit Shape,	1	with	Loculation of Ovary,	3

CHARACTERS WHICH MAY OR MAY NOT BE LINKED

Leaf Margin,	8	with	Loculation of Ovary,	3
Leaf Margin,	8	with	Endocarp Color,	4
Leaf Margin,	8	with	Foliage Color,	10

Since not all the possible combinations of the 6 factors have been tested, and 4 of the factors have not been tested at all, either in combinations among themselves or with any of the other 6 factors, the possibilities of linkage in the tomato have only begun to be examined. It is noteworthy that none of the 7 combinations which either do or do not show linkage are at variance with the interpretation of linkage according to the chromosome hypothesis. For instance, where one of two linked genes is unlinked with a third, the other linked gene is also unlinked with it. This is a necessity on the chromosome hypothesis.⁵

To fit the facts to the chromosome hypothesis it is only necessary to assume that genes 1 and 7 are located in one chromosome which we may call A; genes 3 and 10 must be located in another chromosome, B; gene 4 must be located in a third chromosome, C. Gene 8 can not be in A but may be located in B, C or a fourth chromosome. With these assumptions all the data so far obtained fall into line and if these data are substantiated the other results predicted must hold if the chromosome hypothesis is correct. It must be noted that many of the cases cited here are not fully established on account of the small numbers, and furthermore there is the possibility that what is taken to be independent assortment may be crossing over of about 50 per cent.

⁵ This may also be a necessity on the reduplication hypothesis or may even be axiomatic and must hold for any and every hypothesis that might be put forth to account for factorial linkage.

Since the chromosome number is comparatively low ($1n=12$, Winkler, quoted after East, 1915) the tomato is rather favorable plant material in which to study linkage.

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GENETICS VERSUS PALEONTOLOGY

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ALTHOUGH the title of this article has a somewhat controversial sound, its purpose is merely to discuss, in a perfectly frank and appreciative way, certain passages in the recent works of two eminent geneticists, Professor William Bateson and Professor T. H. Morgan.

"Naturally," says Professor Bateson,¹ in describing a certain theoretical *impasse* as regards the method of evolution, "we turn aside from generalities. It is no time to discuss the origin of the Mollusca or of Dicotyledons while we are not even sure how it came to pass that *Primula obconica* has in twenty-five years produced its abundant new forms almost under our eyes."

Taken in connection with other passages, this seems to imply the belief that the present is no time to investigate phylogenetic problems or to formulate any generalities concerning the origin of systematic groups of organisms. Until the facts of heredity are explained we should turn aside from most of the major problems that engaged the attention of the great comparative anatomists and paleontologists of the nineteenth century. The origin of paired limbs, the origin of the vertebrates, the mutual relations of the great phyla of invertebrates, and similar phylogenetic problems in botany, all these and hundreds more of the same category having been laid aside by the majority of zoologists, are dead or moribund subjects which a student of genetics had better leave in decent obscurity. If Professor Bateson had said "I turn aside from generalities. I have no time to discuss the origin of the Mollusca or of Dicotyledons. I used to be interested in such things, but now I would much rather study the mutations of *Primula obconica*," nobody could reasonably object; but when he says "*we* turn aside from generalities. It is no time [for any one] to discuss the origin of the

¹ *Science*, N. S., Vol. 40, 1914, p. 294.

Mollusca . . .," etc., he is apparently mistaking a part for the whole, and also confusing two fairly distinct lines of investigation, genetics and phylogeny.

As long as museums and universities send out expeditions to bring to light new forms of living and extinct animals and new data illustrating the interrelations of organisms and their environments, as long as anatomists desire a broad comparative basis for human anatomy, as long as even a few students feel a strong curiosity to learn about the course of evolution and the relationships of animals, the old problems of taxonomy, phylogeny and evolution will gradually reassert themselves even in competition with brilliant and highly fruitful laboratory studies in cytology, genetics and physiological chemistry. Very likely the fortunate few who gain some first-hand knowledge in all these fields will realize that such problems as the origin of the Mollusca or the origin of the Dicotyledons have as much vitality as the problem of the origin of the earth or the problem of the phyletic relationship of man with the lower animals.

The student of the evolution of the vertebrates may well reserve judgment as to theories of evolution, and he must even confess his inability to trace a detailed phylogenetic succession except for short intervals; yet he is well assured, from long experience with the paleontological record and with the comparative anatomy of recent animals, that he can trace in a general way the history of many groups and of many structures, and he should know very definitely where the evidence is fairly complete and where it is weak and lacking. In view of the wealth and detailed character of the evidence (which is hardly known except to a limited number of specialists) no competent authority would doubt, for example, that all the races of modern Equidae, walking on the tips of their one-toed feet, have been derived from three-toed *Hipparion*-like forms, or that these in turn lead back to *Eohippus*-like forms of the Eocene, with four digits on each forefoot and three on each hind foot; or that during the Tertiary Period the molar teeth of horses (in the broadest sense) changed

from low-crowned teeth of simple pattern into long-crowned teeth of a complex pattern. And even in the practical absence of paleontological evidence it is sufficiently established that the Cetacea, which are now of pelagic habit and fish-like habitus, represent transformed terrestrial or littoral quadrupeds, which at a remote epoch were placental mammals of some sort. Nor can it be justly doubted that birds are "glorified reptiles," that bats are volant derivatives of arboreal mammals, that teleosts have been derived from ganoids. Detailed knowledge of the evidence in hundreds of such cases leads the paleontologist to say with considerable confidence: "this later type of animal has probably been derived from that earlier type; this structure has undergone such and such changes during certain geological periods."

Professor Bateson is equally cold towards outworn notions about adaptation. "Naturalists may still be found," he says,² "expounding teleological systems which would have delighted Dr. Pangloss himself, but at the present time few are misled. The student of genetics knows that the time for the development of theory is not yet. He would rather stick to the seed-pan and the incubator."

Two very distinct ideas seem to be implied in this passage and the context, first the rejection of the supposed principle of progressive adaptation in evolution, and secondly the idea that conclusions regarding evolution should be limited to those in which control experiments can be made.

As to the principle of progressive adaptation, it is an indisputable fact that existing animals possess structures which are highly efficient in the performance of certain functions, *e. g.*, the locomotive apparatus of the horse, effective for progression over hard ground; its masticatory apparatus, effective in the trituration of siliceous vegetation. Paleontologists, after studying the phylogenetic history of such structures, must infer that progressive advance of structure has been influenced to a

² *Ibid.*, p. 293.

greater or lesser degree by environmental conditions. It is certain that changes in the conditions of life are not the sole causes of modification, it is highly probable that the chromosomes are insensitive to most somatic reactions to the environment; yet how can the student of the Cetacea, who sees how thoroughly the ancestral quadrupedal heritage has been overlaid by the fish-like habitus, doubt that in the end, and perhaps in some very indirect way, the pelagic environment has conditioned the line of evolution of the cetacean chromosomes, as it plainly has conditioned the evolution of cetacean cytoplasm. And when similar adaptations are produced among widely separate stocks, it can scarcely be doubted that the similar results are due to the similarity of the external conditions as well as to the fundamental similarities of all cytoplasm and of all chromatin. Hence, without any commitment as to the mode of evolution, paleontologists adopt the principle of progressive and retrogressive adaptation to environmental conditions as sufficiently demonstrated. And most paleontologists would probably recognize that the foot, for example, is just as much a part of the environment of the femur as is the medium upon which the foot rests, in other words that evolution of a given structure is conditioned by its internal environment as much as by external environment.

Yet such is the skepticism which sometimes results from modern studies in genetics that I have known graduate students who seriously doubted the reality and value of the principle of progressive and retrogressive adaptation, on the ground that, as natural selection and the inheritance of "acquired" characters had both been disproved, there was no conceivable means whereby adaptation could be brought about! But if these skeptics would study for example the evolution of Triassic ganoids into Cretaceous and modern teleosts, if they would consider in detail the structural improvements in the locomotive apparatus of teleosts, which involve the transformation of scales into dermal rays, or of a heterocercal tail into a homocercal tail, or if they would examine the evidence

bearing upon the evolution of the paired limbs or upon the evolution of the vertebrate skull, or of the carnassial teeth of Carnivora, they would, I believe, be forced to accept the principle of the progressive efficiency of structures for special functions as at least a fruitful working hypothesis.

A distrust of the word "adaptation," which has been in the bad company of the Lamarckian theory, is apparently revealed in Professor T. H. Morgan's "A Critique of the Theory of Evolution" (1916). The author, however, apparently favors the idea of natural selection operating upon "advantageous" or "beneficial mutations" and eliminating the "injurious effects" of other mutations. Of course if "adaptation" really implied an acceptance of the Lamarckian theory it would be better to use some such phrase as "progressive functional adjustment," but the important point to bear in mind is that nature has produced myriads of structures which have a very definite functional adjustment with other structures, in other parts of the body, or with parts of other bodies, or with parts of the environment. And it is perfectly plain from the evidence of comparative anatomy and paleontology that functionally correlated parts have often evolved together, and with definite reference to each other, let the explanation of that fact be what it may. Professor Morgan himself has fully recognized this fact in his address³ entitled "Chance or Purpose in the Origin and Evolution of Adaptation."

The second idea which seems to be implied by Professor Bateson, and which I have heard certain university students express, is that phylogenetic "speculations" are unverifiable, because "control experiments" are not possible. By similar reasoning geological theories concerning the history of the earth, archeological theories concerning the history of peoples, and all historical studies based upon internal or circumstantial evidence are equally untrustworthy. The answer to such a theoretical objection, if it were definitely made, would be that comparative

³ *Science*, Vol. 31, 1910, pp. 201-210.

anatomy, geology, phylogeny, etc., are practical arts which have to be learned by experience. Phylogenists must constantly distinguish between primitive and specialized characters, and if their experience, caution and judgment be adequate they may be as successful as physicians are in diagnosis. Of course physicians make mistakes and so do phylogenists, but in the long run both succeed in sifting the false from the true, even without the aid of direct experimentation. Nature herself often provides control experiments, as when she forces animals of widely different stocks into similar life habits, or when she takes a primitive type of skull and dentition and molds them into a wide variety of adaptive types, meanwhile preserving the original pattern as a "control," either in the form of a "living fossil," persisting in a primitive environment, or in the form of a real fossil found in Tertiary strata.

Professor Morgan makes a serious and important criticism of the comparative anatomical and paleontological doctrine that structures have been derived by progressive continuous stages. He is evidently inclined to think that structures have rather been derived through discontinuous mutational stages. It would be easy, he shows, to arrange a graded series of fruit flies belonging to distinct mutations, having at the one extreme perfectly formed wings and at the other extreme no wings at all. But this series by no means represents the historical order of appearance of these mutants, which are not genetically derived one from the other, but have arisen independently. Again (p. 13)

... it is easily possible beginning with the darkest eye color, sepia, which is deep brown, to pick out a perfectly graded series [of races] ending with pure white eyes. But such a serial arrangement would give a totally false idea of the way the different types have arisen; and any conclusion based on the existence of such a series might very well be entirely erroneous, for the fact that such a series exists bears no relation to the order in which its members have appeared.

"Suppose," he continues, "that evolution 'in the open' had taken place in the same way, by means of *discontinuous* variation. What value then would the evidence [for

evolution] from comparative anatomy have in so far as it is based on a continuous series of variants of any organ?"

We may readily admit that *if* evolution in the open has taken place through discontinuous variation, the supposed evidence for evolution based on continuous series of variants is valueless. But neither Professor Morgan nor the present writer try to persuade students of the truth of evolution upon the ground that supposedly continuous series have been traced purporting to illustrate the evolution of *single* structures. As he well intimates, the strongest evidence for evolution is the fact that all the widely diverse members of each group exhibit a common heritage or ground-plan of homologous structures. When that common ground-plan is recognized and when the probable habits of the ancestral form are clearly perceived a long step has been taken toward deciphering the evolutionary history of the group; and it will often be easy to decide what characters and habits have been lost and what new ones have been acquired.

Whether we think evolution has taken place by means of discontinuous variation or through regular progressive and continuous series one of the chief aims of zoologists is, or should be, to discover the facts concerning the phyletic interrelationships of groups and the evolution of their habits and structure. And often the chief earlier and later stages might be recognized in spite of "discontinuous variation." For example, if one knew nothing about the history of the mutant races of *Drosophila* it would seem a safe inference that the apterous form had been derived eventually from a winged type, because a comprehensive study of Diptera in general would indicate that wingless flies were degenerate and not primitive in that respect. Similarly if the systematic relationships and probable derivation of *Drosophila* were given due consideration the races with imperfect eyes and those with duplicated parts would naturally be regarded as degraded or aberrant, rather than original or primary types; and if many intermediate stages between winged and wingless

forms were found living at the same time in a restricted area one might perhaps have suspected that these contemporaneous intermediate forms were parallel offshoots of a normal parent stock rather than linear descendants one of another.

It may well be true that, until it can be shown that evolution "in the open" is continuous and not discontinuous, all "laws" and "principles" which merely assume such continuity are open to question. But there is considerable evidence for the conclusion that many races of mammals have evolved either quite continuously or by small *successive* gradations. It is true that in some cases apparently new and distinct forms also appear in successive horizons, but these new forms may be immigrants from other distribution centers⁴—the little-modified descendants of indigenous races being often found side by side with their more progressive immigrant relatives.

The great collections of American Eocene and later mammals which have been brought together by the systematic explorations of the American Museum of Natural History are all exactly recorded as to level, so that except in a few instances there can be no doubt whatever as to the chronological sequence of the specimens. These collections, numbering many thousands of specimens, are being minutely studied by several investigators, who are not trying to prove any theory of evolution, but are recording and identifying specimens and analyzing their observations, with such accuracy and judgment as they may have gained from twenty years of experience in this work.

The results of these studies, as bearing on the question of continuity *vs.* discontinuity in evolution, are too extensive and complex to be summarized here, but a few examples may serve to illustrate the kind of evidence available and the conclusions which have been drawn in typical instances.

Very often as we pass from lower to higher strata of

⁴ Matthew, W. D., "The Continuity of Development," *The Popular Science Monthly*, Nov., 1910, pp. 473-478.

a given formation the successive species show a regular increase in size and a progressive molarization of the pattern of one or more of the premolar teeth. A typical case of this kind is recorded by Matthew⁵ in the genus *Cynodontomys*, a small insectivorous mammal of the Lower Eocene which is represented by three successive species which do not overlap in time, but are separated by small progressive differences in the premolars and molars. Each species is represented by series of from ten to twenty specimens, from successive horizons of the Bighorn and Wind River Basins in Wyoming. Another instance of practically continuous evolution is furnished by the Middle Eocene titanotheres *Palaeosyops*. Professor Osborn and the present writer have observed that in this genus the species named *paludosus*, *major*, *leidy* and *robustus* form a regular and nearly continuous series extending from the lower to the higher levels of the Bridger Basin, in which the lower and upper premolars gradually evolve toward the molar pattern. A fifth species, *P. copei*, from the uppermost fossiliferous levels of the Bridger Basin is considerably more advanced than any of its predecessors, and is connected with them by intermediate specimens from the nearby Washakie Basin of the same age.

In other cases the material indicates that while some phyla evolve at a nearly uniform rate others lag behind at varying rates, the extreme cases furnishing the relicts or "living fossils" which give so many useful hints as to the primitive characters of a race.

Such an instance is furnished by the history of the Eocene primates *Pelycodus* and *Notharctus* (Table I). The oldest species, *Pelycodus ralstoni*, is of small size and very primitive character. The latest species, *Notharctus crassus*, is about twice as large and of very advanced character. Many intermediate stages are known. Of these *P. relictus* is an extremely conservative form which has acquired only a few of the progressive characters seen in its contemporaries.

⁵ Bull. Amer. Mus. Nat. Hist., Vol. XXXIV, 19, p. 470.

TABLE I

PROGRESSIVE INCREASE IN THE LENGTH OF THE LOWER MOLARS (m_{1-3}) IN
LOWER AND MIDDLE EOCENE LEMUROIDS OF THE FAMILY ADAPIDÆ
(SUBFAMILY NOTHARTINÆ)

Data for Lower Eocene species compiled from Matthew (*Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIV, 1915, p. 436. Data for Middle Eocene species by Granger and Gregory.

MIDDLE EOCENE	HORIZONS UPPER BRIDGER Bridger Basin, Wyo.	{ <i>pm</i> ⁴ with two large external cusps, <i>N. crassus</i> <i>m</i> ¹⁻³ with large mesostyle, 20.7-23.5 mm. molars quadritubercular.							
	LOWER BRIDGER Bridger Basin, Wyo.	<i>P. re-</i> lictus 15	<i>N. for-</i> mosus 16.6	<i>an-</i> ceps 17.5	<i>ty-</i> affinis 18	<i>ty-</i> rannus 18 est.	<i>tene-</i> brosus 18.6	<i>ros-</i> tratus 19	<i>pug-</i> nax 20.7
LOWER EOCENE	LOST CABIN Wind River Basin, Wyo.	<i>Notharctus nunienus</i> 15.5					<i>N. venticolus</i> 18-19.2		
	ALMAGRE* (San Juan Basin, N. M.)								
	LYSITE Bighorn Basin, Wyo.	<i>Pelycodus frugivorus</i> 14-16					<i>P. jarovii</i> 19		
	UPPER GRAY BULL Bighorn Basin, Wyo.	<i>P. frugivorus</i>					<i>P. jarovii</i> 16-18		
	LOWER	<i>P. trigonodus</i> 15					<i>P. jarovii</i> (rare)		
		<i>P. ralstoni</i>							
	SAND COULÉE Clark's Fork Basin, Wyo.	<i>Pelycodus ralstoni</i> 11-14 mm.					{ <i>pm</i> ⁴ with 1 external cusp, <i>m</i> ¹⁻³ without mesostyle, molars tritubercular.		

* The upper levels of the Almagre of New Mexico are perhaps equivalent to the Lysite. Granger, *Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIII, 1914, p. 207.

In certain cases the paleontological evidence is indecisive, as between the hypothesis of successive mutation *in loco* and the hypothesis of continuous evolution in an unknown center of evolution followed by discontinuous immigration of later stages into the region under observation. Such a case is described by Matthew⁶ as follows:

⁶ *Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIV, 1915, p. 316.

Osborn in 1902 pointed out the evolutionary progress observable in the species of *Hyopsodus* from successive stages of the Lower and Middle Eocene; this is in general confirmed and extended by the far larger collections [comprising more than a thousand specimens] now available and the somewhat wider geologic range of the genus; but it is evident that not one but three or four phyla are present in each horizon; the relations of the Lower Eocene species to those of the Middle Eocene are not wholly clear, and the geological overlap of stages of each structural phylum suggests rather progressive displacement of older by newer stages coming in from some other region, than gradual evolution *in loco*. It might equally well be interpreted as the displacement of older by newer "mutants," in the DeVriesian sense of the term.

However this may be, the Lower Eocene species are distinguished from those of the Middle Eocene by the less molariform premolars, and this is most noticeable in *H. simplex* from the lowest horizon, while the Lost Cabin species [from the upper part of the Lower Eocene] approach nearest to those of the Bridger [Middle Eocene].

Examples of this kind might be multiplied, tending to show that the evolution of Tertiary mammals has often been more or less continuous, or by small successive changes, at least during the relatively brief geological periods that are represented by a large series of specimens from closely sequent levels of an uninterrupted stratigraphic series. And although mutations may well be a paleontological reality, there is little danger that vertebrate paleontologists are likely to draw false inferences regarding the history of structures and of races through mistaking independent contemporaneous mutants for successive stages, for the simple reason that their observations are based on long series of specimens which are arranged in their true chronological sequence, from ascending geological horizons covering the whole Tertiary Period.

In this connection I submit an accurate diagram (Fig. 1) by Mr. Granger, which is fairly representative of the kind of evolution demonstrated among many, but not all, known races of mammals during the Tertiary and Quaternary Periods, a period of time conservatively estimated at 4,000,000 years.

The character of the evidence tending to show that the paleontologist is dealing with truly successive stages and

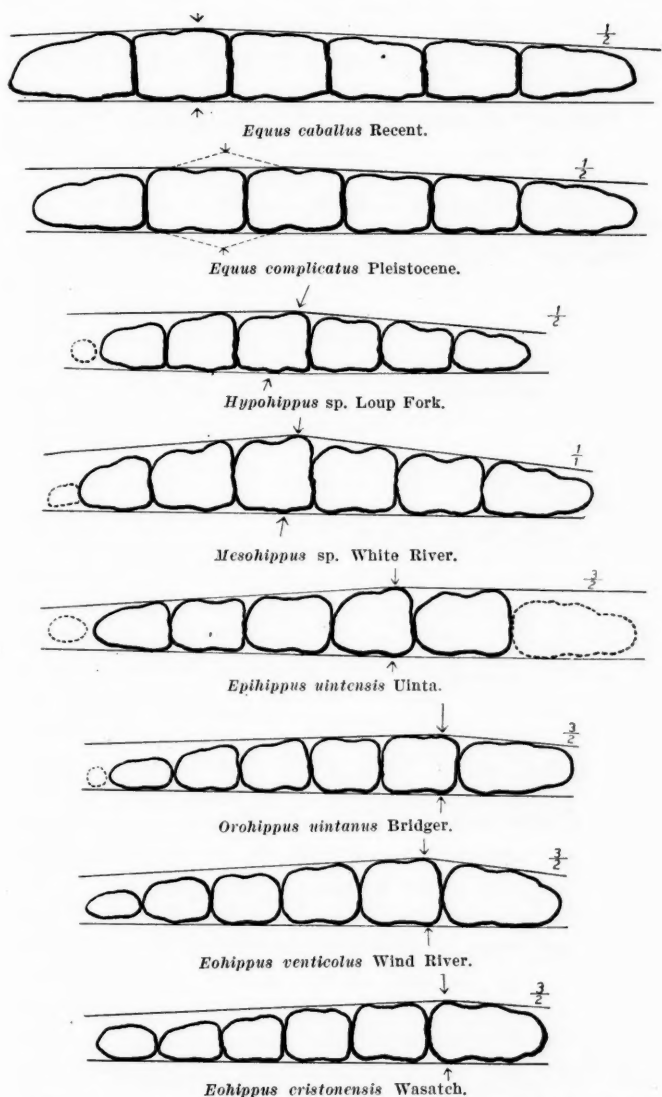


FIG. 1. Accurate outlines of lower cheek teeth of Equidae. Arrows indicate point of greatest transverse diameter in each series, ranging from the third molar in the Wasatch species to the third premolar in the modern Equidae. After W. Granger (*Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, Art. XV, pp. 221-264, 1908.)

not with an arbitrarily selected series of mutants is further illustrated in the following note by Dr. Matthew.

Of the hundreds of specimens examined no horse from the Lower Eocene has ever been found which had *any* fully molariform premolars. No horse out of the Middle Eocene has either more or less than *one* molariform premolar in the lower jaw, on each side. Out of the Upper Eocene all horses have *two* molariform premolars. In the Oligocene all have *three*. All Oligocene and older horses have brachyodont molars without cement. All Miocene horses are progressively hypsodont with a progressive increase in the amount of cement. The milk teeth of Miocene horses have almost no cement. Those of all Pliocene and later horses are heavily cemented. At each successive stage of evolution the cement appears at an earlier stage in the ontogeny of the tooth. These are simply a few out of many progressive changes in the teeth, and they are accompanied by equally clear progressive changes in the skull and skeleton. Every one of these progressive stages is as exactly limited in time as the ones cited.

Geneticists who are examining the nature of the paleontological evidence regarding modes of evolution would do well to realize that only a small part of the available material bearing on the subject is either exhibited or published. The scientific staff of the American Museum of Natural History would be very glad to exhibit to their colleagues the great wealth of accurate data, concerning the chronological sequence of specimens, which has been gathered during twenty years of close exploration; they would also be pleased to place before them any of the extensive series of specimens, sometimes amounting to several thousands of individuals, which appear to throw light upon the problem of continuity *vs.* discontinuity.

In conclusion, paleontologists can show that evolutionary changes have involved *progressive and measurable emphases or suppressions of earlier structures or of earlier proportions* (allometric evolution, Osborn); and when the progressive emphases are manifested as focal outgrowths they seem like "new" structures (rectigradations, Osborn). Paleontologists, however, are not in a position to say which characters would be transmitted according to the Mendelian ratio, nor can they prove what were the cytological causes of the evolutionary changes

which they record or infer. In that direction lies opportunity for consultation with the men who study enzymes, chromosomes, heredity and variation.

The Batesonian hypothesis that both the progressive differential emphases or suppressions of organs, and the focal outgrowth of new structures, have been due to a secular, differential stopping down of inhibitory factors inherent in the germ-cells seems to the present writer quite consistent with the observed facts of evolutionary change; but apparently no observations that the paleontologist can make could furnish any critical tests of this hypothesis; it therefore has for him a stimulative philosophical value, but hardly constitutes a working hypothesis for the discovery of new facts and principles in his limited field.

The nature of later events being determined in part by the nature of their precedent events, no matter how many causal series may be interwoven in the final outcome, it follows that paleontologists, like other historians, contribute to a partial understanding of existing conditions merely by arranging past events in their true chronological sequence. The characteristics of existing Cetacea are determined in part by the germinal and somatic characteristics of their remote quadrupedal ancestors, as well as by the conditions of the pelagic life into which they somehow drifted; so too the characteristics of man, as a bipedal, bimanous, anthropoid Primate are determined in part, as I believe, by the fact that the remote ancestors of the man-greatape stock were arboreal, quadrumanous, lemuroid Primates of the Lower Eocene.

For such reasons, I must continue to hold that "progressive adaptation" when cleared of all implications as to the mode of evolution, stands for a historical and verifiable process; that the time for developing phylogenetic conclusions and for revising comparative anatomy and classification is always *now*, as fast as the evidence can be gathered and analyzed.

SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING. VIII. A SINGLE NUMERICAL MEASURE OF THE TOTAL AMOUNT OF INBREEDING¹

1. In the earlier numbers of these Studies, and particularly in VII,² methods have been given for measuring the amount or degree of inbreeding exhibited in a particular pedigree by a series of inbreeding coefficients, $Z_1, Z_2, Z_3, \dots, Z_n$, one for each ancestral generation. The inbreeding for the whole pedigree is indicated by an inbreeding curve, formed by plotting and connecting by a line the several coefficients.

2. From the earliest stages of this investigation the writer has been aware of the desirability of a *single* numerical measure, to supplement or replace the inbreeding curve as a designation of the total inbreeding exhibited. Such a designation has now been found, which, it is believed, uniquely and rigorously meets the requirements. It is the purpose of the present paper to describe this new constant.

Consider Fig. 1. This gives, in the heavy line and solid circles, the inbreeding curve for 9 ancestral generations of the Brown Swiss bull, Saxton (2668).³ The values of the inbreeding coefficients are:

$$\begin{array}{lll} Z_1 = 0, & Z_4 = 12.50, & Z_7 = 26.95, \\ Z_2 = 0, & Z_5 = 17.19, & Z_8 = 28.91, \\ Z_3 = 6.25, & Z_6 = 21.09, & Z_9 = 29.30. \end{array}$$

The smooth curve of Fig. 1 is the inbreeding curve for continued brother \times sister mating. This represents the closest or maximum degree of inbreeding possible in sexually reproducing organisms.

It is clear from inspection of this diagram, that Saxton is much less intensely inbred in fact than he would be if in all his ancestry the matings had been of brother \times sister out of brother

¹ Papers from the Biological Laboratory of the Maine Agricultural Experiment Station. No. 118.

² Pearl, R., AMER. NAT., 1917, in press.

³ Cf. Pearl, R., these Studies, I. AMER. NAT., Vol. XLVII., p. 603, 1913.

× sister, etc. This is evident, in the first place, because the ordinates of the Saxton curve, $a c$ are nowhere as high as those of the brother × sister curve, $a b$. But it would also be equally clear that Saxton was less inbred than the maximum possible amount if the last ordinate at c , for example, had a value of 99.6, as does the corresponding ordinate of the maximum curve.

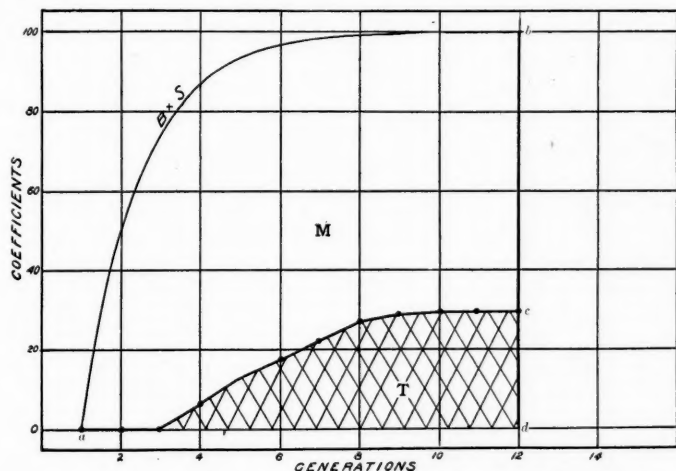


FIG. 1. Diagram showing the inbreeding curve of Saxton, a Brown Swiss bull, in the heavy lines and solid circles. The smooth, light line curve is the curve of maximum inbreeding (continued brother × sister breeding). For further explanation see text.

Upon consideration it appears that the real measure of comparative amount or degree of inbreeding, considering the pedigree as a whole, is given by the *area* included by the particular inbreeding curve under discussion, as compared with the corresponding area of the maximum (brother × sister) curve. Thus in Fig. 1, Saxton is less inbred than the maximum possible amount to an extent proportionate to the amount by which the area T ($a c d$) is smaller than the area M ($a b d$). This consideration gives us the desired method of uniquely expressing the total amount or degree of inbreeding. It only remains to consider practical methods of calculation.

3. Theoretically one should integrate the maximum (brother × sister) curve, and the observed curve, and compare the areas derived from such integrations. Practically this is not possible, because many observed curves of inbreeding can not be fitted by

any simple, readily integrable theoretical curves. We shall hence be compelled in this case to make use of the expedient so frequently employed in applied mathematical problems of all sorts, namely, to take finite summation as a sufficiently close approximation to integration. Doing so, we may take as the simple expression of total inbreeding, to and including the n th generation, the following:

$$\frac{Z_{T_n}}{100} = \frac{\sum_{Z_1}^{Z_n}}{F_{T_n}}, \quad (i)$$

where Σ denotes summation of all values between the inclusive limits indicated, and F_{T_n} is a constant having the value set forth in Table I. F_{T_n} is of course the total area of the maximum brother \times sister curve up to and including the $n + 1$ -th generation. Since these successive values are constant they may be tabled once for all.

TABLE I

VALUES OF F_{T_n} , THE INCLUSIVE AREAS OF THE MAXIMUM INBREEDING CURVE

Ancestral generation	n	F_{T_n}
2	1	50
3	2	125
4	3	212.5
5	4	306.25
6	5	403.125
7	6	501.5625
8	7	600.78125
9	8	700.390625
10	9	800.1953125 ⁴
11	10	900.09765625
12	11	1000.048828125
13	12	1100.0244140625
14	13	1200.01220703125
15	14	1300.006103515625
16	15	1400.0030517578125

In using the form of total inbreeding coefficients shown in (i) there is one caution which must be carefully observed. This is that only so many generations should be used as to include the one in which the observed Z taken first reaches its highest value for the pedigree under discussion, and not any beyond that one. This will usually be for the earliest ancestral generation of the pedigree, but not always.

⁴ One would not, of course, use in practical calculation such excessive numbers of decimals as are tabled from this point on.

4. We may now consider some numerical illustrations. Let us take first the bull Saxton, for which the several observed inbreeding coefficients have already been given. We have

$$\Sigma Z_i = 142.19$$

and hence, from Table I,

$$Z_{T_3} = \frac{14219}{800.1953} = 17.8.$$

Or we may say that Saxton is inbred in ten ancestral generations, taken together 17.8 per cent. of the maximum amount possible in those generations.

For comparison some other figures may be examined. Pearl and Patterson⁵ have given mean values of the inbreeding coefficients for four groups of Jersey cattle: (a) Random sample bulls, (b) register of merit bulls, (c) random sample cows, (d) register of merit cows. It will be of interest to reexamine these figures by the method here described. The results are given in Table II.

TABLE II

TOTAL INBREEDING COEFFICIENTS FOR JERSEY CATTLE. (PEARL AND PATTERSON DATA)

Group	Total Inbreeding Coefficients Z_{T_i}		
	Lower Limiting Values	Upper Limiting Values	Mean
1. General population (random sample) bulls	25.39	30.48	27.94
2. Register of merit bulls.....	24.52	29.17	31.85
3. General population (random sample) cows	27.46	31.74	29.60
4. Register of merit cows	20.72	27.08	23.90

From this table we see that American Jersey cattle, as judged by random samples of the general population, are about 28 to 30 per cent. as closely inbred as the maximum possible amount, taking account of the first eight ancestral generations *as a whole*.

It is not desirable to go further into the discussion of these Jersey data, since the purpose of this note is simply an exposition of method. This new method makes possible exact and unique numerical comparison between pedigrees in respect of the degree of inbreeding which they exhibit in the same number of ancestral generations.

RAYMOND PEARL

⁵ Pearl, R., and Patterson, S. W., *Proc. Nat. Acad. Sci.*, Vol. 2, p. 60, 1916.